

Effects of Herbivory and Proximity to Surface Water on C and N Dynamics on the Elk Winter Range in Rocky Mountain National Park

By

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Abstract. It has been suggested that recent increases in elk herbivory and changes in hydrology towards drier conditions have contributed to declines in willow (*Salix* spp.) communities in the winter ranges for elk in Rocky Mountain National Park (RMNP). During the fall of 1994, we constructed 12 large elk exclosures in two watersheds of the elk winter range in RMNP, and conducted field experiments during the growing seasons of 1995 to 1999 to investigate the effects of herbivory and proximity to surface water on the dynamics of carbon (C) and nitrogen (N). We found that elk herbivory led to increases ($P < 0.05$) in N concentration of willow litter and decreases in litterfall biomass, but herbivory did not affect losses of C and N from litter in any of the growing seasons. Soil moisture levels were higher in lower landscape positions, which probably led to higher ($P = 0.001$) C losses from litter, in comparison to upper landscape positions. In plots where N fertilizer was added, we observed an increase ($P < 0.05$) in willow shoot length, shoot biomass, and the average amount of N in the shoots, indicating that availability of N is limiting plant growth in our study sites. Elk herbivory had no effect on soil inorganic N availability and *in situ* net N mineralization rates, maybe because of the short time since treatment establishment (4 years). However, we estimated that the return of N to the soil in grazed plots could be as much as 265% of the N return in exclosed plots, due perhaps to N transfers from the summer range to the winter range. Our results demonstrate that elk herbivory and proximity to surface water have significant influences on the biogeochemical cycles of the winter ranges for elk in RMNP. Greater return of N to the soil, combined with increased litter quality in the grazed plots, indicate that elk could contribute to increases in N cycling rates and availability in the long-term, which could lead to changes in ecosystem structure and function in the winter range for elk in RMNP.

Keywords: Browsing, *Carex*, grazing, litter, nitrogen availability, *Salix*, willow.

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Introduction

Since 1968, elk (*Cervus elaphus*) numbers in Rocky Mountain National Park (RMNP), Colorado, have been managed under a policy of natural regulation, which rests on the assumption that density-dependent mechanisms would result in equilibrium between large ungulate herbivores and plant resources. During this period, elk numbers increased from approximately 700 to about 3,000 animals, and park managers are concerned about the effects these increases will have on the soils and vegetation of the elk winter range within the park (Singer et al. 1998a).

Willow (*Salix* spp.) communities have reportedly been declining on elk winter ranges of RMNP during the last few decades (Hess 1993; Singer et al. 1998b), and similar declines have also been reported for Yellowstone National Park (YNP) (Chadde and Kay 1991; Kay and Wagner 1994; Singer et al. 1998b). In addition to increased elk herbivory, two other factors have been proposed to explain these declines in willow communities: (1) climates are warmer and drier this century, possibly resulting in lowered stream flows and less water availability to plants (Singer et al. 1998b); and (2) beaver populations have declined on the eastern slope of RMNP (Stevens and Christianson 1980), which may further contribute to the drying of these ecosystems.

Large herbivores can significantly influence plant community structure and biogeochemical cycles within the soil-plant system (Frank et al. 1994; Frank and Groffman 1998; Hamilton et al. 1998; Schuman et al. 1999; Wijnen et al. 1999). Herbivores can influence nutrient cycling by removing plant biomass and returning more readily available nutrients to the soil (McNaughton et al. 1988; Frank et al. 1994; Hamilton et al. 1998), increasing soil nitrogen (N) mineralization rates and plant N uptake (Frank and Groffman 1998; Wijnen et al. 1999), and spatially redistributing nutrients within the landscape (McNaughton 1985; Afzal and Adams 1992; Russelle 1992). In some N-limited systems, herbivory may lead to slower rates of nutrient cycling due to increases in the dominance of non-browsed plant species, which may produce litter with low nutrient concentrations or with high concentrations of secondary compounds (Pastor et al. 1993; Ritchie et al. 1998). In addition, herbivory can influence plant growth and physiology (Toft et al. 1987; Welker and Briske 1992; Singer et al. 1998a,b; Fahnestock and Detling 1999) and alter carbon (C) and N allocation within plants (Welker et al.

1985, 1987; Holland and Detling 1990; Singer et al. 1998a; Alstad et al. 1999). Changes in the root:shoot ratio following browsing may lead to improvements in the water balance of plants (Welker and Menke 1990), while the removal of meristems (Briske 1986) or overgrazing (Pengelly 1963; Singer et al. 1998a) may reduce their future growth potential. Whether herbivory has a positive or negative influence on plants may depend in part on the specific characteristics of each system (Georgiadis et al. 1989; Hamilton et al. 1998; Mazancourt et al. 1998; Alstad et al. 1999).

Beaver (*Castor canadensis*) can also influence plant communities and biogeochemical cycles of ecosystems. By building dams, beavers contribute to the entrapment of sediment and organic matter and modify nutrient cycling and decomposition dynamics (Naiman et al. 1986). Active beaver ponds may increase N and phosphorus (P) inputs to the flooded systems (Naiman and Melillo 1984) and increase water availability to plants, which enhance the conditions for willow growth and reestablishment of shoots, sprouts, and seedlings (Naiman et al. 1986; Singer et al. 1998b). It has been suggested that the observed declines in beaver populations on the eastern slope of RMNP have contributed to a decrease in the surface area of water (ponds and streams) within the winter range of elk since the beginning of this century (Singer et al. 1998b). These reductions in surface water may alter the biogeochemical cycles of those ecosystems, and could further reduce the ability of willow to respond to elk herbivory.

Plant-available N is usually a limiting element for plant growth in terrestrial ecosystems (Power 1977; Kiehl et al. 1997; Wijnen et al. 1999). The cycling of N in these systems is linked to the C cycle by internal organic matter transfers and positive and negative feedback loops between decomposers, plants, and herbivores (Aber and Melillo 1991; Pastor and Naiman 1992). Therefore, the dynamics of C and N are of critical importance to primary productivity and overall ecosystem function (Power 1994; Schuman et al. 1999). There is no available information about the effects of elk herbivory or the reduction in surface water on the dynamics of C and N in the winter ranges of elk in RMNP. This information is necessary to help park managers formulate policies that will maintain elk and beaver populations at levels that are adequate for preserving the natural functioning of these ecosystems. Therefore, the objective of this study was to perform experimental field manipulations to investigate the effects of elk herbivory and proximity to surface water on the C and N cycles of the winter ranges of elk in RMNP.

Methods

Study Sites

The low elevation winter range for elk in RMNP encompasses about 17,000 ha, which includes land within the eastern side of the park and private and national forest lands outside the park in the town of Estes Park and Estes Valley, Colorado (Singer et al. 1998b). Our study sites were located in two riparian ecosystems on the northeastern side of RMNP: Moraine Park (Big Thompson River watershed, elevation 2,481 m) and Horseshoe Park (Fall River watershed, elevation 2,598 m). The two watersheds are within 5 km of each other and have perennial alpine snowfields at their headwaters. Mean annual precipitation for the sites is 41 cm (Singer et al. 1998b) and peak stream flow usually occurs in early to mid-June (USDA 1995, 1996, 1997). The 30-year average temperature for the adjacent Estes Valley ranges from 9°C to 17°C during the 5-month growing season of May through September (Alstad et al. 1999). The study area consists of wet meadows dominated by willow (*S. monticola*, *S. geeyeriana*, and *S. planifolia*), other shrubs such as birch (*Betula* spp.), sedges (*Carex* spp.), rushes (*Juncus balticus*), and grasses (*Phleum* spp., *Calamagrostis* spp., *Bromus* spp., *Poa* spp.). The wintering elk population numbers about 3,000 animals, of which about one-third generally spends the winter within the park (Larkins 1997; Singer et al. 1998b).

Experimental Treatments

In the wet meadows of both parks, twelve 30 m x 46 m exclosures were erected within willow communities along the rivers between August and November of 1994. Next to each exclosure, 30 m x 46 m plots were chosen and marked off as paired plots open to grazing (grazed plots). Each site consisted of an exclosure and a grazed plot. Eight sites (four in Moraine Park and four in Horseshoe Park) were placed in areas with little or no current beaver activity, and contained heavily browsed willow (short willow). The other four sites (two in each park) were located in wetter areas, generally containing taller willow plants subjected to less severe browsing by elk (tall willow). In half of the short willow sites (two in each park), hydro-manipulation treatments were imposed by placing sheet metal check dams on ephemeral stream

channels both inside the exclosures and in the grazed plots (short-watered willow). We expected these check dams to catch snowmelt and rain runoff through the spring and raise the water table at the sites. Twenty-five dams were installed in April and May 1995 and were relatively successful in holding additional water at these sites. The dams were intended to add water, but the treatment was unable to simulate water additions in the amounts accomplished by beaver dams on larger, permanent streams (Singer et al. 1997). The other four exclosures in short willow sites were left to normal hydrologic regimes (short-control willow). In each exclosure and associated grazed plot, an average of five shallow (0.5 m to 2 m) wells were installed in the spring of 1995 for the purpose of monitoring groundwater levels. During early 1996 and 1997, three dams were constructed by beaver near two sites within the wetter area of Moraine Park, but these dams were washed out during the spring floods of 1996 and 1997.

The area within each exclosure was sub-divided in 15 x 23 m sub-plots and two treatments were imposed throughout the period of the study: (1) 75% current annual growth (CAG) removal (clipped plots); and (2) no clipping at all (ungrazed plots). Additionally, elk browsed willows outside the exclosures (grazed plots). The 75% CAG removal treatment was applied between January and April of 1995, 1996, 1997, and 1998, and consisted of clipping all forage shrubs and herbaceous plants in each sub-plot. All clipped plant biomass was removed from the exclosures.

Litterfall

Litter was collected in each experimental plot during the fall of 1995, 1996, and 1997, through the use of 15 greenhouse trays (totaling ~2.3 m²) arranged in a 5 x 3 regularly spaced grid (9.1 x 15.9 m). The grids were established randomly within each sub-plot before willow senescence began, and each tray was anchored to the ground using two or more large spikes. Litter was collected weekly from early September to late October until litterfall was complete. The litter was then composited within each experimental replication, sorted by genus and litter type, air dried, and weighed. Oven-dry corrections were applied within each category by drying a subsample at 60°C. Litterfall biomass was calculated as oven dry mass per unit area. Total N and C content of litter was determined using a LECO CHN-1000 analyzer.

Litter Decomposition

During September and October of 1994, we collected litter material to generate a standard litter that was used in the decomposition experiments. Willow leaf litter was collected by locating greenhouse trays directly under willow canopies. Graminoid litter was collected by clipping and collecting dead biomass throughout the study area. We dried all litter in a 35°C forced air oven, and subsamples (2 g) from the two standard litter types (willow leaves and graminoid tissue) were enclosed in 1 mm nylon mesh bags. The bags were used in litter decomposition experiments to investigate the effects of herbivory, landscape position, and plant cover on the decomposition rates of willow and graminoid litter during the 1995, 1996, and 1997 growing seasons. In all experiments, the litterbags were left in the field during the entire length of the growing season (from late May until mid-September), and then collected, air-dried, weighed, ground to a fine powder, and stored until analysis. Carbon and N in the decomposed litter were analyzed using a LECO CHN-1000 analyzer, and C and N losses were calculated on an ash-free dry weight basis by subtracting the amounts in the pre-decomposition from the post-decomposition litter.

During the growing season of 1995, four bags of each litter type (willow leaves and graminoid tissue) were randomly placed within the exclosures in the ungrazed plots and outside the exclosures in the grazed plots for all 12 sites. In 1996 and 1997, in each of the ungrazed and grazed plots, we selected two willow shrubs located at two different landscape positions: (1) lower landscape positions, next to a stream or a pond; and (2) upper landscape positions, at least 10 m away from a stream or pond and 0.5 m higher in the landscape than lower landscape positions. Bags of both willow and graminoid litter were placed under the canopies of the selected willow and in open grass areas next (within 2 m) to the shrubs. Two bags of each litter type were placed within each treatment replication in order to reduce microsite variability.

Elk Dung Quantification

We estimated the amount of C and N returned to the soil in elk dung by counting the number of scat piles along 30 m transects within our experimental grazed plots, and measuring the concentrations of C and N in the dung. The survey was conducted after the elk herds left the winter range for the summer range during late

spring 1997. We selected eight grazed plots (four in each park) and established four randomly placed transects per plot. In each transect, we measured the distance from the scat piles to the transect, and calculated the density of piles per area. Only scat piles that were visually identified as from the previous fall and winter were counted. In order to estimate dry matter and C and N content in each dung pile, we obtained 51 samples (26 from Horseshoe Park and 25 from Moraine Park) by collecting all dung from fresh piles during late fall of 1997. After collection, the samples were air-dried, weighed, ground to a fine powder, and sub-sampled for determination of moisture and ash content. The concentrations of C and N in the dung were determined using a LECO CHN-1000 analyzer and expressed on an ash-free dry weight basis.

Soil Characteristics and N Availability

Soil samples (0 to 15 cm) were collected in July 1997 from the grazed, ungrazed, and clipped plots. Within each treatment replication, 25 to 30 cores were randomly collected with a soil core sampler 2 cm in diameter and combined in a paper bag. After collection, the samples were taken to the laboratory, air-dried, and passed through a 2 mm sieve. Soil particle distribution was measured in each sample using the hydrometer method (Gee and Bauder 1986). Sub-samples (10 g) of each sample were ground to a fine powder with a ball mill. The sand fraction (>53 μ m) of each sample was ground to a fine powder with a ball mill, for determination of particulate organic matter (POM) C and N (Cambardella and Elliott 1992). Total C and N in the total soil and sand fraction were determined with a LECO CHN-1000 analyzer. Soil pH was measured in a 2.5:1 (water:soil) suspension.

In addition, during the summer of 1996, we collected soil samples (0 to 20 cm) under willow trees and in associated open grass areas within 2 m to the trees. A total of 35 pairs of samples (shrub canopy plus open grass) were taken from the 12 ungrazed plots within the exclosures of Moraine Park and Horseshoe Park. The samples were air-dried and sieved through a 2 mm screen. Sub-samples (10 g) of each sample were ground to a fine powder with a ball mill, and total soil C and N were determined using a LECO CHN -1000 analyzer.

Soil moisture (0 to 14 cm) measurements were performed weekly in eight sites in Moraine Park and Horseshoe Park (four in each watershed) by Time Domain Reflectometry (TDR) (Ledieu et al. 1986) with

a Trase System model 6050x1 during the 1997 growing season. Within each site and grazing treatment, soil moisture was measured under willow canopies and in associated graminoid plots next to the willow shrubs in both upper and lower landscape positions.

Within three ungrazed plots in each park, soil temperature was measured using HOBO® temperature data loggers during the 1997 growing season. The data loggers were wrapped with a thin plastic film to avoid damage by soil moisture, and buried in a vertical position from 1 to 6 cm depth. In each of the sites, we performed comparisons of soil temperature between: (1) willow canopies and graminoid plots; and (2) streamside (lower) and upper landscape positions. The temperature measurements were performed every 15 minutes for periods of 7 to 14 days.

In 1995, 1996, and 1998 soil *in situ* N availability in the experimental plots was assessed using ion-exchange resin bags. Paired cation and anion resin bags made from nylon stockings and containing about 15 cm³ of exchange resins were placed 5 cm beneath the soil surface (Binkley 1984). In 1995 and 1996, 15 pairs of resin bags were placed in a regularly spaced grid (9.1 m x 15.9 m) within each treatment (grazed, ungrazed, clipped) in the 12 sites. In order to analyze the temporal variability of N availability, two sets of bags were placed in each treatment during the 1995 and 1996 growing seasons. The first set was left in place from mid-June to mid-July, and the second set from mid-July to mid-August. A different experimental procedure was utilized in 1998, in which six pairs of resin bags were randomly placed within each of the 12 ungrazed and grazed plots, and left in the field from May to October. For all 3 years, after removal of the bags, the N adsorbed in the resins was extracted with 50 ml of 2 M KCl, and the extracts frozen until analysis on an Alpkem automated spectrometer.

In 1997 and 1998, *in situ* measurements of net N mineralization were performed by conducting field soil incubations as described in Kolberg et al. (1997) using aluminum cores 15 cm long and 5 cm in diameter. During the 1997 growing season, cores were placed in upper and lower landscape positions within the 12 ungrazed and grazed plots of the two watersheds. Within each landscape position and grazing treatment, cores were placed under willow shrubs and in associated graminoid patches within 2 m of the willow plants. Four cores were placed inside each treatment replicate in order to reduce micro-site variability. Cation and anion resin bags were placed in the bottom of each core to capture the inorganic N leached from the core. During the 1998

growing season, six open-top field soil incubation cores were placed within the ungrazed and grazed plots in three different 6-week incubation periods (June to July, July to August, and August to October). Net soil N mineralized during the incubation periods was calculated by subtracting the initial amount of inorganic N in the soil from the final amount of inorganic N after the incubations, and the results were expressed in g N m⁻².

Nitrogen Fertilization

In each ungrazed and grazed plot in the 12 sites, we placed two paired circular subplots (each with 2 m radius) around willow plants at the end of the 1998-growing season. Within each pair of circular subplots, we applied two fertilization treatments: (1) no fertilization, and (2) 10 g N m⁻² as ammonium nitrate. During late July 1999, willow shoots (CAG) were collected from the plants inside the subplots, dried at 60°C, weighed, and ground to a fine powder. Concentrations of C and N in shoots were determined using a LECO CHN -1000 analyzer.

Statistical Analyses

Statistical analyses were performed using the SAS Statistical Package (SAS, Version 6.12, SAS Institute Inc., Cary, NC, 1995). There were no significant interactions at any level including watershed, willow height, and hydro-manipulations. Therefore, the data from the experiments on litterfall, litter nutrient content, soil characteristics, and elk dung deposition were analyzed for the effect of elk herbivory using a randomized complete block design. The data from the experiments on litter decomposition and soil N availability were analyzed using a split-plot design with herbivory manipulations as the main treatment and landscape position or canopy position as sub-plots.

Results and Discussion

Litterfall

Litterfall biomass in the ungrazed and clipped plots was greater ($P < 0.05$) than in the grazed plots for the three growing seasons (Table 1). Across all growing seasons, litterfall biomass averaged 65.6 and 33.0 g m⁻² inside and outside the exclosures, respectively. On average, willow leaves accounted for 58% of the litterfall biomass followed by herbs (20%), other shrub leaves

Table 1. Litterfall biomass in ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park during 1995, 1996, and 1997. Values represent means ($n = 12$) with standard errors in parentheses. Means within the same group followed by different letters are significantly different at $P < 0.05$.

Treatment	Litterfall (g m ⁻²)					All litter
	Willow (<i>Salix</i> spp.) leaves	Other shrub leaves ¹	Herbs ²	Wood	Unidentified material	
1995						
Ungrazed	32.9 (9.8) ^a	5.9 (2.7) ^{a,b}	10.1 (2.4)	3.0 (1.0)	0.6 (0.2)	52.5 (10.2) ^a
Clipped	34.1 (8.5) ^a	13.2 (6.3) ^a	8.0 (1.0)	4.4 (1.4)	0.3 (0.1)	60.0 (8.9) ^a
Grazed	19.1 (7.1) ^b	1.7 (0.6) ^b	6.4 (0.9)	3.1 (1.4)	0.5 (0.2)	30.9 (8.5) ^b
1996						
Ungrazed	55.0 (13.6) ^a	9.1 (3.9) ^{a,b}	3.1 (0.6)	3.1 (1.1)	1.4 (0.4)	71.6 (12.6) ^a
Clipped	47.1 (10.6) ^{a,b}	18.3 (8.6) ^a	2.6 (0.5)	1.6 (0.4)	0.8 (0.2)	70.2 (9.7) ^a
Grazed	26.6 (8.1) ^b	3.7 (0.8) ^b	3.4 (0.5)	5.1 (2.2)	0.7 (0.3)	39.4 (9.1) ^b
1997						
Ungrazed	45.3 (12.3) ^a	8.7 (4.0) ^{a,b}	14.3 (3.3)	3.1 (1.0)	-	71.5 (11.1) ^a
Clipped	41.6 (10.4) ^a	15.5 (6.3) ^a	7.2 (0.7)	2.2 (0.7)	-	66.4 (10.1) ^a
Grazed	15.9 (6.0) ^b	3.0 (0.9) ^b	7.5 (1.0)	2.4 (1.1)	-	28.8 (7.1) ^b

^{a,b,c}Denote significant differences ($P < 0.05$).

¹Mostly birch (*Betula* spp.) leaves.

²Litter material from forbs and graminoid combined.

(16%), wood (5%), and unidentified material (1%). However, the use of trays for collecting litterfall may underestimate the amount of grass litterfall, since a significant portion of the senescent tillers still remain attached to the plant and were not collected and counted as litter. Willow leaf litterfall in the ungrazed and clipped plots was greater ($P < 0.05$) than in the grazed plots during the 1995 and 1997 seasons, but in 1996 there were no significant differences between clipped and grazed plots (Table 1). Leaf litter from other shrubs, mostly birch (*Betula* spp.), was significantly lower in the grazed plots when compared to the clipping treatment inside the exclosures, but there were no differences between grazed and ungrazed plots. No grazing treatment differences were observed for the amounts of herb or wood litter during the three growing seasons.

Litterfall biomass was lower in the grazed plots, in comparison to the clipped and ungrazed plots, due to elk browsing during early fall before leaf senescence. However, inside the exclosures, even the removal of 75% of CAG in the clipped plots did not result in significant

differences between the ungrazed and clipped plots during the three growing seasons. We suggest this lack of difference between clipped and ungrazed plots occurred in part because the artificial clipping of willow did not satisfactorily simulate elk browsing. Other studies have demonstrated the limitations of clipping experiments to reflect accurately the natural patterns of herbivory (Paige 1999). Visual observations in our field plots suggested that clipped plants inside the exclosures were morphologically similar to the plants in the ungrazed treatment, regarding height and canopy structure, while the grazed plants were apparently more suppressed and shorter than the plants in the two treatments inside the exclosures. These patterns probably resulted from the additional damage to willow leaders caused by elk when stripping off leaves from the plants, as compared to artificial clipping. On average, elk may browse on more than 70% of the leaders in each plant in our study sites, and may remove nearly 40% of the length of each leader (Singer et al. 1998b). Additional field observations from our experiments demonstrate that an

average of 20% of the length of browsed willow leaders may die after elk browsing due to bark damage, while only 2% of the length of the leader may die in the case of artificially clipped plants (R. Peinetti, Natural Resources Ecology Laboratory, personal communication). We suggest that the differences in growth and litterfall observed between grazed and clipped treatments in our study may result from: (1) greater leader damage during elk browsing, in comparison to artificial clipping; and/or (2) greater increases in plant height in clipped plants, in comparison to grazed plants, due to differences in the patterns of tissue removal during elk browsing or artificial clipping, which may influence canopy architecture. Overall, we suggest that the clipped plants in our study were able to overcompensate for the biomass removal and achieve greater fitness, in comparison to browsed plants, but additional studies are needed to test this hypothesis.

Willow leaf litter in the ungrazed and clipped plots had lower ($P < 0.05$) N content and higher ($P < 0.05$) C to N ratio than willow leaf litter in the grazed plots, but no significant treatment differences were found in litter from other shrubs, graminoids, or forbs (Table 2). Similar to our findings, Alstad et al. (1999) reported that early season willow tissue N concentration in plants under elk herbivory in our sites was significantly higher than in plants protected from herbivory. Often, grazing leads to increases in plant tissue N (McNaughton 1985; Holland and Detling 1990; Coughenour 1991; Hamilton et al. 1998) due to faster nutrient cycling and uptake by plants or a reduction in tissue biomass for allocation of N. Higher N concentration and lower C to N ratios in litter may lead to faster litter decomposition and greater nutrient availability (Irons et al. 1991; Ritchie et al. 1998). In our study site, the effects of elk herbivory on willow litter N concentration could lead to increases in the rate of litter decomposition and nutrient cycling, which could lead to changes in species composition and ecosystem functioning (Aber and Melillo 1991; Holland et al. 1992; Ritchie et al. 1998; Stohlgren et al. 1999).

Litter Decomposition

Grazing had no effect on the decomposition of willow and graminoid litter in any of our experiments, but C and N losses between willow and graminoid litterbags were significantly different. In the three growing seasons, C losses from willow litterbags were higher ($P < 0.05$) than from graminoid litterbags (Table 3). Interestingly, N losses from willow litter were lower than from graminoid litter (Table 3), perhaps

because willow litter has a higher content of secondary compounds or promotes greater N immobilization during decomposition, when compared to graminoid litter. Browsed willow plants may increase the concentration of secondary defense compounds, such as tannins, as a response to prevent further herbivory (Singer et al. 1994). The standard litter utilized in our decomposition studies had a relatively high concentration of tannins, averaging 70.7 mg g^{-1} dry matter⁻¹ (Cates, et al., this volume). Our findings indicate that, even though willow litter has a lower C to N ratio when compared to graminoid litter, the presence of secondary compounds in willow litter may have caused a significant reduction in the losses of litter N when compared to graminoid litter.

In 1996, C losses from litterbags were higher ($P = 0.001$) in streamside positions than in upper landscape positions, but no significant differences were observed for N losses during 1996 or C and N losses during 1997 (Table 4). Soil moisture is usually an important factor contributing to decomposition and, in general, litter decomposition increases with increasing soil moisture in semi-arid ecosystems (Schlesinger 1997). Higher C losses observed in streamside positions in our study are likely due to higher soil water availability (Fig. 1). However, no significant differences in willow or graminoid litter decomposition were observed between streamside and upper landscape positions around the two beaver ponds in 1996. Average C and N losses from litterbags of the two litter types placed around the ponds were 36.4% and 2.9%, respectively. The lack of consistent differences in litter decomposition between different landscape positions in our experiments may have occurred because 1996 and 1997 had higher rainfall levels than the long-term average for those sites (Alstad et al. 1999). For these reasons, the differences in soil moisture may not have been as pronounced between landscape positions as they would have been in drier years, especially towards the end of the growing season, as indicated by the increases in soil moisture in July 1997 (Fig. 1).

Litterbags placed under willow canopies lost significantly more C and N than bags placed in graminoid plots (Table 5), even though soil moisture levels were slightly lower under willow canopies, compared to graminoid plots, especially in Horseshoe Park (Fig. 1). Average maximum soil temperatures from 1 to 6 cm in depth during the 1997 growing season were significantly lower under willow canopies than in graminoid plots in both Moraine and Horseshoe Parks (Fig. 2). These results indicate that the presence of willow shrubs has a significant influence on microclimatic conditions in our

Table 2. Nitrogen content and carbon to nitrogen ratio of different litter types in ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park in 1997. Values represent means ($n = 12$) with standard errors in parentheses. Means within the same group followed by different letters are significantly different at $P < 0.05$.

Treatment	Willow (<i>Salix</i> spp.) leaves	Other shrub leaves ¹	Graminoids	Forbs
Nitrogen (%)				
Ungrazed	1.25 (0.10) ^b	1.23 (0.15)	1.40 (0.11)	1.79 (0.13)
Clipped	1.27 (0.09) ^b	1.11 (0.13)	1.22 (0.08)	1.71 (0.15)
Grazed	1.49 (0.08) ^a	1.09 (0.11)	1.23 (0.09)	1.82 (0.12)
Carbon to nitrogen ratio				
Ungrazed	45.8 (3.2) ^a	48.5 (12.0)	37.2 (2.9)	31.0 (3.0)
Clipped	43.0 (4.2) ^a	53.4 (11.6)	42.1 (2.8)	32.6 (2.9)
Grazed	37.7 (3.1) ^b	49.9 (14.3)	43.5 (3.1)	31.4 (2.6)

¹Mostly birch (*Betula* spp.) leaves.

^{a,b}Different letters denote statistical differences at $P < 0.05$.

Table 3. Carbon and nitrogen losses from willow (*Salix* spp.) and graminoid leaf litter bags in Moraine Park and Horseshoe Park during the growing seasons of 1995, 1996, and 1997. Values represent means ($n = 12$) with standard errors in parentheses.

Litter type	% C loss	% N loss
1995		
Willow	30.2 (2.7)	6.3 (2.0)
Graminoid	22.9 (2.6)	10.3 (2.1)
P-value	n.s. ^a	0.026
1996		
Willow	29.0 (1.9)	3.4 (5.1)
Graminoid	22.9 (2.4)	15.2 (4.7)
P-value	0.046	0.005
1997		
Willow	22.1 (1.4)	2.7 (2.4)
Graminoid	16.4 (1.8)	16.4 (4.3)
P-value	0.013	0.005

^aNot significantly different at $P < 0.05$.

Table 4. Carbon and nitrogen losses from litter bags placed in upper and lower landscape positions of Moraine Park and Horseshoe Park during the growing seasons of 1996 and 1997. Values represent means ($n = 12$) with standard errors in parentheses.

Landscape position	% C loss	% N loss
1996		
Streamside	31.7 (2.3)	5.7 (6.1)
Upper landscape	20.3 (1.9)	12.8 (6.0)
<i>P</i> -value	0.001	n.s. ^a
1997		
Streamside	18.1 (1.9)	6.5 (4.2)
Upper landscape	20.4 (1.3)	12.9 (2.7)
<i>P</i> -value	n.s.	n.s.

^aNot significantly different at $P < 0.05$.

sites, contributing to reductions in soil temperature and soil moisture. We suggest that the rate of nutrient loss from litterbags was higher under willow canopies because: (1) shading by willow canopies may decrease soil temperature and increase soil moisture at the top few centimeters of the litter layer and soil. This may enhance litter decomposition, and/or (2) graminoid plants may have supported litterbags off of soil in open sites, which may have let them dry out more and decompose less than bags placed under willow canopies.

Return of N to the Soil

Based on the biomass and N content of aboveground litter in our sites (Tables 2 and 3), we calculated that the N return to the soil in litterfall during the 1997 growing season was greater ($P < 0.05$) in the ungrazed and clipped plots (0.83 and 0.82 g N m⁻², respectively) than in the grazed plots (0.42 g N m⁻²), excluding the contribution of N in wood litter in all treatments. Similar to our findings, Pastor et al. (1993) found that moose browsing led to decreases in the amount of litterfall and nutrient return to the soil in litter. In our site, litter from willow, other shrubs, and herbs contributed to 62%, 17%, and 21% of the N returned to the soil inside the exclosures, and 51%, 16%, and 33% of the N returned to the soil in grazed plots, respectively. Elk dung biomass deposited on the soil during the 1997–1998 season averaged 42.2 ± 6.2 g m⁻² across all sites. This value is similar to those reported by Frank and McNaughton

(1992), who found that average herbivore dung deposition during the 5-month season in the winter range of YNP was 76.9 ± 30.1 g N m⁻². In our sites, average elk dung N concentration in the samples collected in late fall of 1997 was 2.0%. Based on our results, we estimated that approximately 0.87 ± 0.12 g N m⁻² was returned to the soil in elk dung during the 1997–1998 winter season in our study site. Therefore, the amount of N returned to the soil as elk dung plus plant litter averaged 1.3 g m⁻² in the grazed plots. The estimated amount of N returned to the soil in elk urine in our sites, based on the diet and specific characteristics of the herd, could be approximately 98% of the N returned to the soil in dung (Schoenecker et al., this volume). Based on these estimates, after including the potential N inputs from urine, the total amount of N returned to the soil in the grazed plots could be as high as 2.2 g N m⁻², which corresponds to 265% of the N returned as aboveground litter in the exclosed plots. Our results are consistent with the findings of Frank and McNaughton (1992), who found that elk and bison populations in YNP excreted 0.81 to 4.60 g N m⁻² yr⁻¹, an amount that corresponded to roughly four times the amount of N returned in litterfall. In addition, those authors concluded that the intensity of herbivory was positively associated with both aboveground net primary production and the return of nutrients to the soil.

Ungulates usually accelerate nutrient cycling by modifying the amount and quality of residues returned to the soil (Hobbs 1996). Similar to the findings of Frank

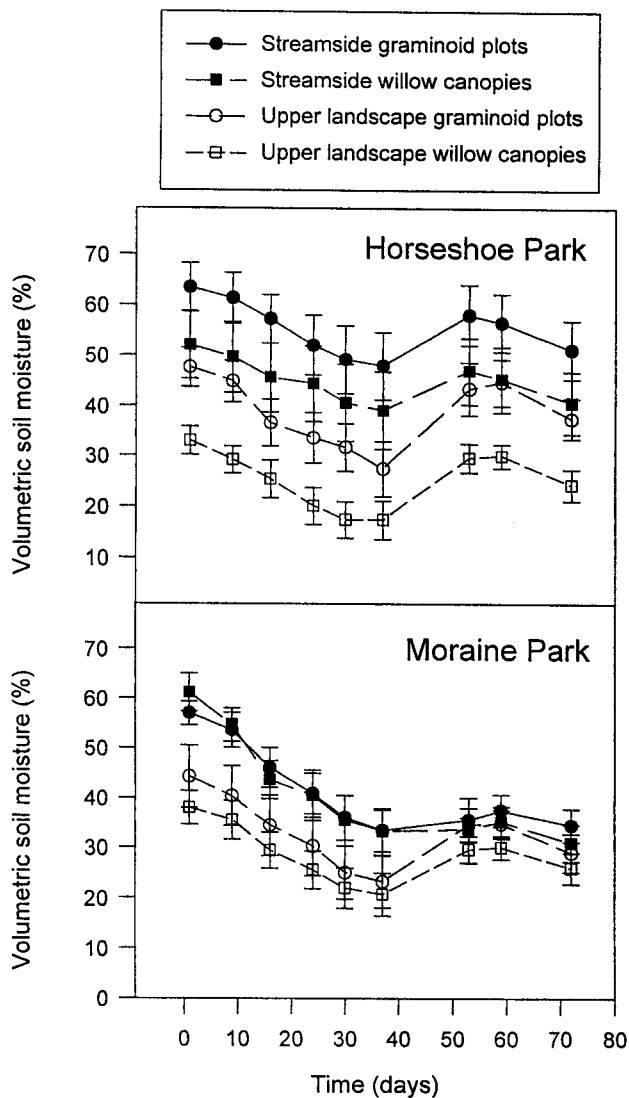


Fig. 1. Soil moisture (0 to 14 cm) under willow canopies and in graminoid plots in upper and lower landscape positions of Horseshoe Park and Moraine Park from early June to late August of 1997. Error bars represent standard errors of the means ($n = 8$).

et al. (1994) in Yellowstone, a portion of the excess N returned to the soil by elk in our study sites may correspond to transfers from the summer range. During winter, elk migrate from the summer range to the winter range at lower elevations to avoid snow and usually lose weight and N (F. Singer, U.S. Geological Survey,

Table 5. Carbon and nitrogen losses from litter bags placed under willow (*Salix* spp.) canopies and in graminoid plots in Moraine Park and Horseshoe Park during the growing seasons of 1996 and 1997. Values represent means ($n = 8$) with standard errors in parentheses.

1996	% C loss	% N loss
Willow canopies	35.7 (1.7)	24.2 (1.8)
Graminoid plots	7.7 (2.9)	-1.6 (2.4)
<i>P</i> -value	0.001	0.022
1997		
Willow canopies	23.1 (1.5)	15.5 (1.7)
Graminoid plots	16.0 (3.5)	3.4 (3.5)
<i>P</i> -value	0.00	0.012

personal communication). Our results indicate that elk may be promoting a net transfer of N from the summer range to the winter range, and the extent of these transfers are likely related to the number of elk in this system. In the long-term, these N transfers could increase N availability, which in turn may affect ecosystem structure and functioning (Aber and Melillo 1991; Holland et al. 1992; Ritchie et al. 1998; Stohlgren et al. 1999).

Soil Characteristics and N Availability

There were no significant differences ($P < 0.05$) in total soil C and N, POM C and N, soil texture, and soil pH between grazing treatments in our sites within the 4 years after the establishment of the exclosures (Table 6). Similar to our findings, Frank and Groffman (1998) found no differences in soil total C and N between grazed plots and exclosed plots that had been protected from herbivory for 33 to 37 years in YNP. However, Frank and Groffman (1998) found that herbivores improved the quality of soil organic matter, increasing the labile fractions and decreasing the recalcitrant fractions. In our study, the relatively short time (4 years) since the establishment of the exclosures may not have allowed for the development of significant differences in the organic matter fractions between herbivory treatments. In addition, we found no differences in total soil C and N (0 to 30 cm) between soil samples taken in graminoid plots or under willow canopies. Total soil C and N

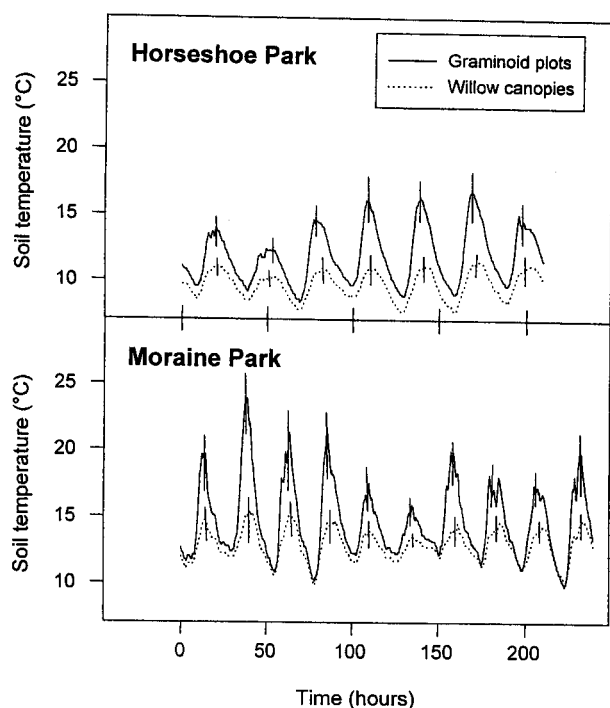


Fig. 2. Soil temperature (1 to 6 cm) under willow canopies and in graminoid plots in Horseshoe Park and Moraine Park during July 1997. Vertical lines represent the range of the 95% confidence interval for the means of maximum temperatures ($n = 3$).

averaged 6.2 and 0.44 g kg⁻¹ in graminoid plots and 5.8 and 0.40 g kg⁻¹ under willow canopies, respectively.

In all experiments with both ion-exchange resin bags and field soil core incubations, there were no significant differences in soil N availability between grazing treatments during the 4 years of the study. Several studies have reported increases in the rates of soil N mineralization with herbivory (McNaughton 1985; McNaughton et al. 1988; Holland and Detling 1990; Frank and Evans 1997). Frank and Groffman (1998) reported that N availability in plots grazed by elk was 100% higher than exclosed plots. Again, we suggest that the time since the establishment of the exclosures in our study did not allow for the development of detectable differences in soil N mineralization and availability between grazing treatments.

The assessment of N availability with ion-exchange resin bags during 1995 and 1996 indicated that, in general, both NH₄⁺-N and NO₃⁻-N availability were higher ($P < 0.05$) during early to mid-season and declined afterwards (Table 7). In 1998, there was only one resin bag incubation period, and the total amount of N adsorbed to the bags was slightly higher than the sum of both periods of either 1995 or 1996, probably because the incubation period in 1998 was a few weeks longer. On average, the amount of NH₄⁺-N adsorbed to the resin bags was 137 to 412% higher than NO₃⁻-N during the three growing seasons. The higher proportions of soil NH₄⁺-N could benefit plant productivity in our sites, since plants with an evolutionary history of grazing show elevated growth responses to ammonium relative to other

Table 6. Soil characteristics (0–15 cm) of ungrazed, clipped, and grazed plots of Moraine Park and Horseshoe Park in July 1997. Values represent means ($n = 12$) with standard errors in parentheses.

	Total C	Total N	POM C	POM N	Sand	Silt	Clay	
Treatment	g kg soil ⁻¹							pH ^a
Ungrazed	50.3 (9.0)	3.38 (0.63)	15.9 (3.5)	0.81 (0.19)	523 (59)	209 (40)	152 (19)	4.64 (0.10)
Clipped	47.7 (7.1)	3.27 (0.54)	13.3 (2.0)	0.63 (0.09)	494 (55)	235 (47)	161 (25)	4.67 (0.12)
Grazed	42.7 (6.2)	2.82 (0.44)	11.3 (2.0)	0.53 (0.12)	549 (37)	234 (29)	118 (19)	4.60 (0.11)

^aMeasured in water (2:1, water:soil)

Table 7. Inorganic nitrogen adsorbed to ion exchange resin bags during different incubation periods during 1995 and 1996, and one incubation period during 1998. Values represent means ($n = 12$) with standard errors within parentheses.

Incubation period	Inorganic nitrogen (mg bag ⁻¹)		
	NO ₃ ⁻ -N	NH ₄ ⁺ -N	NO ₃ ⁻ -N and NH ₄ ⁺ -N
1995			
June to July	1.08 (0.23)	4.45 (0.63)	5.53 (1.45)
July to August	0.64 (0.32)	2.12 (0.44)	2.78 (1.29)
<i>P</i> -value ^a	0.015	0.001	0.001
1996			
June to July	0.95 (0.52)	3.39 (0.81)	4.34 (1.14)
July to August	1.05 (0.55)	1.44 (0.53)	2.49 (0.87)
<i>P</i> -value	n.s. ^b	0.001	0.001
1998			
July to October	3.01 (0.55)	7.29 (1.98)	10.30 (2.43)

^a*P*-value of comparisons between means of incubation periods.^bNot significantly different at $P < 0.05$.**Table 8.** Inorganic nitrogen mineralized during field soil incubations (0 to 15 cm) using aluminum cores during 1997 and 1998. Values represent means for all treatments ($n = 12$) with standard errors within parentheses.

Incubation period ^a	Mineralized nitrogen (g m ⁻²)		
	NO ₃ ⁻	NH ₄ ⁺	NO ₃ ⁻ + NH ₄ ⁺
1997			
June to July	0.11 (0.04)	0.55 (0.15)	0.66 (0.16)
1998			
June to July	0.71 (0.44)	0.81 (0.80)	1.51 (0.77)
July to August	1.13 (0.38)	1.33 (0.95)	2.46 (1.17)
August to October	0.51 (0.23)	0.34 (0.52)	0.85 (0.59)

^aLength of incubation period: 1997 = 4 weeks; 1998 = 6 weeks each period.

Table 9. Inorganic nitrogen adsorbed to ion exchange resin bags under willow (*Salix* spp.) canopies and in graminoid plots during different incubation periods of the 1995 and 1996 growing seasons. Values represent means ($n = 12$) with standard errors within parentheses.

Position	Inorganic N (mg bag ⁻¹)	
	June to July	July to August
1995		
Willow canopies	5.69 (2.13)	2.87 (1.20)
Graminoid plots	5.80 (1.92)	2.87 (1.11)
<i>P</i> -value	n.s. ^a	n.s. ^a
1996		
Willow canopies	4.98 (0.77)	3.07 (0.55)
Graminoid plots	4.01 (0.68)	2.42 (0.37)
<i>P</i> -value	0.018	n.s. ^a

^aNot significantly different at $P < 0.05$.

Table 10. Effects of nitrogen fertilization on willow (*Salix* spp.) growth and N assimilation during the growing season of 1999. Values represent means ($n = 12$) followed by standard errors between parentheses.

Treatment	Shoot length (cm)	Shoot biomass (g)	Shoot N concentration (%)	Amount of N per shoot (g)
N fertilizer (10 g N m ⁻²)	28.6 (1.4) ^{a,1}	27.3 (2.5) ^a	2.25 (0.05)	0.62 (0.06) ^a
No fertilization	22.5 (1.1) ^b	20.2 (2.4) ^b	2.14 (0.06)	0.43 (0.05) ^b

^{a,b}Different letters denote statistical difference at $P < 0.05$.

¹Means followed by different letters are significantly different at $P < 0.05$.

inorganic forms of N, particularly when subject to defoliation (Ruess 1984; Ruess and McNaughton 1987; Hobbs 1996). Similarly to the results from the experiments with ion-exchange resin bags, the amounts of net NH_4^+ -N mineralized in the soil cores were usually higher than NO_3^- -N (Table 8). In addition, total inorganic N in the soil was higher during early to mid-season during the 1998 growing season (Table 8). If plant uptake is higher during early to mid-season when plant growth and nutrient requirements are probably greater, the higher availability of nutrients during that period may contribute to the synchronization of nutrient supply and demand and enhance primary production and nutrient retention within the system (Myers et al. 1994). Interestingly, the presence of willow had a significant effect on N availability in our experiments with ion-exchange resin bags. During both incubation periods of 1996, the amounts of inorganic N adsorbed to resin bags located under willow canopies was higher ($P < 0.05$) than in bags placed in graminoid plots (Table 9), but no significant differences were observed during 1995. The higher N availability may be a consequence of higher amounts of litter N inputs and higher rates of N loss from litter under willow canopies, as indicated by our findings in 1996.

The data from the N fertilization experiment demonstrated that willow growth in the winter ranges for elk is limited by N availability, independently of grazing treatment. Both inside and outside the exclosures, N fertilizer additions increased ($P < 0.05$) willow shoot length, shoot biomass, and the amount of N in the shoots (Table 10). We suggest that elk herbivory could lead to long-term increases in N availability in our sites, because of induced increases in both litter quality and return of N to the soil. Increases in N availability could lead to changes in plant species composition and significantly alter ecosystem functioning because of shifts in the competitive interactions between plant species (Tilman 1982, 1988; Holland et al. 1992; Sterner 1994; Ritchie et al. 1998). Stohlgren et al. (1999) reported that exotic species were more likely to invade landscape patches with higher soil N and moisture, which could lead to a decline in native plant species and ecosystem diversity (Billings 1990; D'Antonio and Vitousek 1992).

Conclusions

Herbivory by elk significantly influenced the biogeochemical cycles of the winter ranges for elk in

RMNP. Losses of C from litter and soil moisture were greater in streamside positions, when compared to upper landscape patches, indicating that reductions in surface water may lead to lower decomposition rates in our site. Elk grazing reduced the amount of litterfall biomass and the amount of N returned to the soil in litter. However, we estimated that the return of N to the soil through elk excretions plus aboveground litter in the grazed plots could be as much as 265% greater than inside the exclosures, maybe due to transfers of N from the summer range to the winter range. Willow litter contributed to 51% to 62% of the N returned to the soil in litterfall, and grazing by elk significantly increased the N concentration and reduced the C to N ratio of willow litter. We found no differences in soil total C and N, POM C and N, and N availability between grazed and ungrazed plots during the period of our study, maybe because there was not enough time (4 years) to develop significant differences between herbivory treatments. Nitrogen fertilization significantly increased willow shoot length, shoot biomass, and the average amount of N in the shoots, indicating that availability of N is a limiting factor for willow growth in our study sites. Greater return of N to the soil combined with increased litter quality in the grazed plots indicate that elk could contribute to increases in N cycling rates and availability in the long-term in our sites. Increased N availability could lead to changes in plant species composition and ecosystem functioning.

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